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A Note on the Origin of Rodents

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Knowledge of Paleocene rodents is still restricted to a single species, *Paramys atavus*, from a single locality, the Eagle Coal Mine at Bear Creek, Montana. The age of this deposit is late Paleocene. Incisors of *P. atavus* were first described by Simpson (1928, p. 14), but were referred by him to the Multituberculata. Jepsen (1937) recognized the true affinities of the incisors and described a newly found lower molar. No additional material has been reported since 1937. The purpose of the present paper is to place on record the morphology of a recently identified upper cheek tooth of *Paramys atavus* and to discuss briefly its significance. I am indebted to Drs. Albert E. Wood and Mary Dawson for helpful comments. Mr. Chester Tarka prepared the figure.

ORDER RODENTIA

FAMILY PARAMYIDAE

GENUS *PARAMYS* LEIDY, 1871

Paramys atavus Jepsen, 1937

Material: A.M.N.H. No. 22195 (fig. 1), a left P^4, M^1, or M^2, figured by Simpson (1929, p. 10, fig. 2).

Locality: Eagle Coal Mine, Bear Creek, Carbon County, Montana.

Formation: Polecat Bench formation (Fort Union of the United States Geological Survey and others).

Age: Tiffanian (= approximately late, but not latest, Paleocene).

Description: Small, tritubercular, rodent upper cheek tooth with

tiny cingulum hypocone at posterior base of protocone. Paracone massive, triangularly pyramidal; metacone with flat anterolingual face, other faces rounded; protocone high, conical, connected by crests to conules, apex not connected to cingula; conules simple, not multiple; no mesostyle whatever; no trace of a mesoloph; anterior cingulum low, curving to meet paracone apex; posterior cingulum cuspidate, broad, terminating in a small but distinct hypocone; paraconal and metaconal roots small, protoconal root large; enamel smooth (partly but not wholly the result of wear and preservation). Maximum length, 1.5 mm.; width, 1.8 mm.

DISCUSSION: The upper cheek tooth of *Paramys atavus* described here was originally discussed by Simpson (1929, pp. 9–10) more than 30 years ago. The specimen was tentatively designated cf. *Labidolemur* sp., and the latter was referred to the plesiadapid primates. At that time Matthew's family Apatemyidae had been merged with the Plesiadapidae, and *Labidolemur* was generally considered to be close to *Plesiadapis* and *Phenacolemur*. The much closer similarity of *Labidolemur soricoides* and *L. kayi* (now *Apatemys kayi*) to Eocene apatemyids was as yet unrecognized. For these reasons it was not unreasonable for Simpson to turn to *Labidolemur kayi* as a likely bearer of the upper tooth under discussion, especially as the tooth does resemble to a considerable extent the molars of *Plesiadapis*, *Phenacolemur*, and other closely related forms. Abel (1931, p. 273) immediately questioned Simpson's identification, however. Jepsen (1934) cleared up former confusion by separating the Apatemyidae from the Plesiadapidae. His elucidation of apatemyid morphology demonstrates that the apatemyids were a lineage separate from either *Plesiadapis* or *Phenacolemur*, a fact that has been further demonstrated by the discovery of the Torrejonian apatemyid genus *Jepsenella*. The upper cheek teeth of apatemyids are now fairly well known and show no special resemblance to the tooth tentatively referred to *Labidolemur* by Simpson. Moreover, the type of the Bear Creek species referred by Simpson to *Labidolemur* has now been shown (McKenna, 1960, pp. 47–51) to be referable to *Apatemys* itself. In the course of this last work the Bear Creek upper cheek tooth, A.M.N.H. No. 22195, was recognized as a very primitive paramyine rodent tooth.

It is not possible to determine with any degree of certainty whether the upper cheek tooth of *Paramys atavus* is the fourth premolar or one of the anterior molars. Eocene rodent molars frequently depart radically from the structure of the fourth premolar, but an upper molar of a Paleocene rodent would be expected to resemble the fourth upper premolar to a considerable extent. Although the Bear Creek upper cheek tooth resembles

P^4 more than M^1 or M^2 of *Paramys excavatus*, a conservative course is followed here in the hope of avoiding error. The specimen is identified merely as a cheek tooth.

The upper tooth of *Paramys atavus* is, as is the lower molar, a very primitive paramyid tooth, perhaps the most primitive known. The morphology of the crown is remarkably devoid of specializations characteristic of most Eocene rodents, but the major features leave no doubt that the tooth belongs to a small and primitive species of *Paramys*, probably

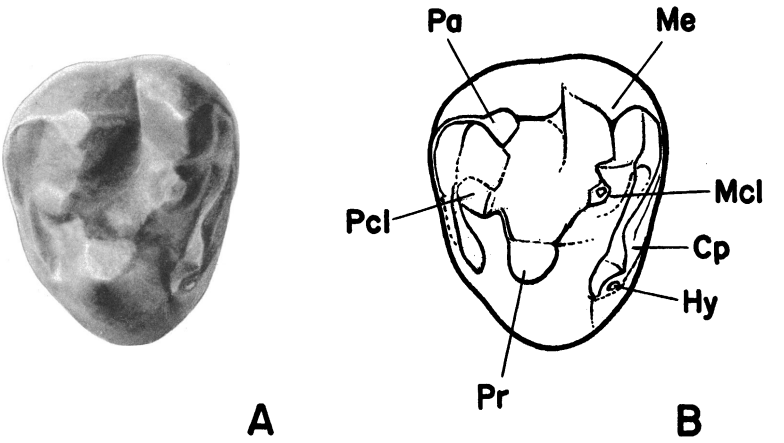

FIG. 1. *Paramys atavus*, A.M.N.H. No. 22195, left P^4, M^1, or M^2. A. Photograph retouched by Chester Tarka. B. Interpretive drawing. *Abbreviations*: Cp, posterior cingulum; Hy, hypocone; Mcl, metaconule; Me, metacone; Pa, paracone; Pcl, protoconule (paraconule). ×20.

related to the Eocene species *P. excavatus*. All later paramyid fourth premolar and molar types could have differentiated from this sort of morphology.

The crown pattern exhibited by the Bear Creek upper cheek tooth is strikingly similar to the hypothetical tritubercular sciurid *grundplan* figured by Stehlin and Schaub (1951, p. 11, fig. 1). The principal difference is that the Bear Creek tooth possesses a tiny hypocone on the posterior cingulum at the posterior base of the protocone. The hypocone is not the posterior half of a dividing protocone such as that suggested for Stehlin and Schaub's hypothetical prosciurid ancestor "*Protadelomys*" (*ibid.*, p. 27, fig. 24). It seems more probable that the connate, subequal protocone and hypocone of *Adelomys cartieri*, some sciuravids, and certain other rodents arose by hypertrophy of an originally small cingulum

hypocone. Nor is the hypocone of the *Paramys atavus* tooth a swelling on the ridge running from the protoconid apex to the posterior cingulum as in many primitive sciurids. Originally, the sciurid condition probably arose by incorporation of the hypocone in the ridge. The pattern shown by *Paramys atavus* seems admirably suited to a member of the paramyid ancestral stock. It could have given rise to many Eocene and later rodent tooth patterns, of which the sciuravid, pseudosciurid, and sciurid patterns seem the most demonstrably derivative at present.

Primitive though it is, the tiny hypocone of *Paramys atavus* is in keeping with the structure of the cheek teeth of most available likely ancestors of rodents in the Paleocene. Pre-Paleocene possible ancestors generally had a wide buccal cingulum, extremely transverse teeth, or both. Although the ultimate ancestry of rodents must trace back to the Cretaceous, the immediate ancestry would seem to trace to animals in the process of minimizing the buccal cingulum and developing a small hypocone at the lingual end of a posterior cingulum. Such animals are abundant in the Paleocene, particularly among primates and certain insectivores (*sensu lato*) related to primates. For these reasons it seems probable that rodents primitively possessed a hypocone, even though the structure was originally small and quite distinct from the protocone. Stehlin and Schaub's hypothetical reconstructions of sciurid and pseudosciurid *grundplans* (*ibid.*, pp. 11, 27) are therefore regarded here as probably incorrect.

Jepsen (1949, pp. 488–489) has emphasized that rodents apparently replaced multituberculates ecologically. In early Wasatchian sediments, both may occur in the same fossil concentration, but where one is common the other is not (McKenna, 1960, pp. 13–25). Such occurrence can be interpreted in two ways: one can assume that the multituberculates and rodents were in direct competition in an essentially uniform environment, quarry sample differences reflecting the ebb and flood of battle; or one can posit that different quarries reflect slightly different habitats, to which now one and now the other was well adapted. In the Eocene, what these ecological differences were is not immediately apparent, but the second alternative seems the more likely of the two. In the Paleocene, the habitat at Bear Creek was definitely unusual. The environment was that of a small coal swamp near the edge of a structural basin, and the most commonly preserved mammal remains are those of an animal currently classified as a primitive colugo or "flying lemur." Whether the animal, *Planetetherium*, is a dermopteran or not is of no importance here. The fact that it is the most common fossil mammal at Bear Creek and occurs nowhere else is of great interest. The complete absence of multituberculates, regardless of whether or not a rodent was present, is amazing for any

Paleocene site. The immediate Paleocene ancestors of *Paramys atavus* may therefore be expected to occur in heretofore unexploited facies of Torrejonian and perhaps Puercan sediments. The ultimate rodent ancestors may occur in more familiar deposits. Specimens of them may already repose unrecognized before our very eyes.

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